THE ORIGIN OF THE LEAFY SPOROPHYTE.

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ATTENTION has been called afresh to this exceedingly interesting and obscure problem by the discussion of alternation of generations by Professor Bower in his recent presidential address,[1] and in papers of Dr. Klebs,[2] and Dr. Lang.[3] The remarks of Professor Bower are largely in defense of his theory of the antithetic origin of the sporophyte, which had been attacked by Dr. Scott in his presidential address of two years before in restating Pringsheim's theory of homologous alternation. In defending his position, Professor Bower discusses arguments derived from the behavior of algæ and certain fungi, from bryophytes, and from apogamy and apospory. He claims that those algæ and phycomycetes which show subdivision of the zygote into spores appear to offer the "key to the enigma" of the origin of the sporophyte, but he makes no further claim for these "fruit bodies" than that they suggest the way in which the sporophyte may have arisen, his view not at all involving the idea that these "fruit bodies" and the sporophyte are homogenetic. He calls attention to the fact that knowledge of cytological phenomena among algæ and fungi is far too meager, especially in connection with the divisions of the zygote referred to. If reduction is found to occur in connection with the zygote divisions, in such forms as Œdogonium and Coleochæte, there would be a reasonable foundation for the belief that the "fruit bodies" are the correlatives of a sporophyte, the beginning of a neutral generation.

In reference to the bryophytes, Professor Bower sees in them a good illustration of the origin of the sporophyte by "a

[1] Nature, Nov. 17, Nov. 24, Dec. 1. 1898.

[2] Annals of Botany **12**: 570–583. 1898.

[3] Annals of Botany **12**: 583–592. 1898.

progressive antithetic alternation." He calls attention to the remarkable constancy of alternation in this group, apogamy and apospory being singularly absent. This undeviating alternation he suggests may be accounted for by the dependence of the sporophyte, which is in an "equable physiological condition." As a contrast to this, the independence of the pteridophyte sporophyte, and its exposure to varied conditions, may have caused more freely unusual developments. The primitive pteridophyte, however, was probably in a dependent condition, as the embryos of modern pteridophytes are.

Apogamy and apospory Professor Bower would regard as "abnormalities," calling attention to the fact that these phenomena have their "headquarters" in the leptosporangiate ferns, a peculiarly specialized phylum with many other abnormalities. Even when apogamy occurs the archegonia are first produced, indicating the "first intention" of the plant; and in both apogamy and apospory the growths may be very anomalous.

In this connection, Professor Bower makes a very interesting suggestion, based upon the experiments of Dr. Lang and others. He observes that apogamy is induced by prevention of contact with fluid water ("rendering fertilization impossible"), exposure to direct sunlight, and possibly to certain temperature conditions. All this leads to a "plethoric" state, which he thinks may be a necessary condition preceding apogamy, as opposed to deficient nutrition, which precedes apospory, the latter being "a physiological refuge for the destitute plant." He suggests that nuclear changes may accompany these conditions, plethora doubling the chromosomes, and hence inducing the development of a sporophyte; and deficient nutrition reducing the chromosomes, thus making a gametophyte possible. Of course it remains to be proved that nuclear instability, coming to be well recognized, is connected with disturbed nutrition, and also whether a smaller or larger number of chromosomes necessarily determine a gametophyte or a sporophyte.

On the whole, therefore, Professor Bower still maintains that the sporophyte is the result of the gradual elaboration of the

zygote, "a fresh phase having thus been gradually interpolated," in other words, that its origin is antithetic. It would seem that in his opinion the sporophyte has probably appeared in just one way. This does not mean that all sporophyte plants are homogenetic, but that all have had an origin similar to that of the sporogonium of bryophytes. Professor Bower acknowledges that the present tendency is toward a comprehensive polyphyletic view as regards alternation, stating that "when difficulties arise refuge is taken in the plausible suggestion of distinct lines of descent."

Dr. Lang's paper is rather a presentation of current views than an expression of opinion in reference to any of them. He recognizes the fact that the regularity of the zygote product in such forms as Œdogonium and Coleochæte represents a life history decidedly different from the homologous alternation of sexual and asexual plants in most thallophytes. From one point of view this zygote product is merely a reduced asexual individual; from another point of view it is not a reduced asexual individual, but a special adaptation to multiply the product of fertilization. The former is the theory of homologous origin, the latter the theory of antithetic origin. Certainly the facts of morphology do not decide which theory is correct. Dr. Lang calls attention to the fact that in considering alternation the possible polyphyletic origin of the archegoniates must be kept in mind, as the pteridophytes may represent an entirely distinct line from the bryophytes, as suggested by Goebel. In spite of Professor Bower's disposition of apogamy as an argument, Dr. Lang thinks that experiments with this phenomenon indicate so clearly that the gametophyte may assume characters of the sporophyte under suitable conditions, almost a complete series of transitions between gametophyte and sporophyte having been observed, that such a general property of the fern gametophyte cannot be disregarded in the discussion, even though the phenomenon may be called teratological. He thinks that apogamy suggests the homology of the gametophyte and sporophyte, and may suggest how pteridophytes could have

been derived from algæ forms, and how alternation in ferns might have arisen if it did not come antithetically.

The paper of Dr. Klebs deals with the subject of alternation of generations in thallophytes, and therefore concerns this present discussion but indirectly. His experiments among the lower forms, as is well known, have proved that there is no such rigidity in life histories as was once supposed. As a consequence, he does not consider that there is any such thing even as a regular homologous alternation of sexual and asexual phases. He thinks that experiments may prove that the so-called "fruit bodies" of such forms as Œdogonium and Coleochæte may turn out to be the result of certain conditions, rather than an inevitable part of the life history. He seems to consider that the origin of pteridophytes probably has nothing to do with that of bryophytes, and that there is at present no clue whatsoever as to the origin of the former. Such a peculiar structure in common as the archegonium he suggests may be a purely parallel development, without necessarily indicating any phylogenetic connection.

It will be seen from the above papers that, while the origin of the sporogonium of bryophytes seems to be suggested, the origin of the leafy sporophyte is too obscure to justify any definite claim. According to Bower it is most probable that it is developed from such a sporogonium structure as is displayed by the bryophytes today; according to Lang and Klebs there is a possibility that it may have had an entirely independent origin, and may never have been in the sporogonium condition.

It is recognized that there are peculiar difficulties in the discussion of such a subject. Although the morphology of the existing representatives of the various groups is fairly well known, there are two enormous gaps in our knowledge which make a definite conclusion impossible. One of these gaps is the ancient history of the bryophyte and pteridophyte lines. For instance, it is certain that the pteridophytes were well represented in the palæozoic, probably even in its earliest periods. This represents such a tremendous stretch of time that almost any change, however extensive, may have been possible in any given form. It is

not through lack of time, therefore, that one would suggest that it is unlikely for a leafy sporophyte to have been developed from a sporogonium. From the fact that our earliest evidences of the pteridophytes show them to have been about as highly differentiated as they are now, it is evident that the evolution of the line reaches very far back. It is probably hopeless to expect that this gap in our knowledge will be filled.

The other gap is in reference to cytological details. The whole subject of alternation of generations seems to be so bound up with nuclear changes that a knowledge of these in the thallophytes becomes a very great desideratum. This gap in our knowledge is likely to be filled up rapidly. It may be that we have been too rigid in our use of the number relations of chromosomes as distinguishing gametophytes from sporophytes. Be this as it may, there is enough in the testimony associating the doubling and the reduction of chromosomes with the sporophyte and gametophyte stages to justify such use. It would seem that an investigation into the nuclear changes which occur in the "fruit bodies" of such forms as Œdogonium and Coleochæte would go far toward settling the antithetic origin of such a structure at least as the sporogonium of bryophytes.

It is not my purpose in this paper to traverse ground which has been gone over so recently and so ably, but merely to discuss certain facts and possibilities in connection with the leafy sporophyte that may be suggestive. In discussing the origin of such a structure as the leafy sporophyte where there is no possible direct evidence, and where every view must be hypothetical, it seems necessary to consider all possible alternatives. The chief service which these various alternatives render is to coordinate the facts and to suggest lines of research.

No structure among plants seems to have left so little trace of its origin as the leafy sporophyte of pteridophytes and spermatophytes. The evolution of the leafless sporophyte of bryophytes seems traceable from an oospore which directly organizes a group of sporogenous cells. Sterilization of the peripheral cells would result in a simple spore case like that of

Riccia, while further encroachment upon the sporogenous tissue, with more or less differentiation of the sterile tissue, would account for the series of sporogonia displayed by bryophytes. Whether the origin of this structure is to be regarded as homologous or antithetic is not pertinent to the present discussion, but it seems reasonable to see in it an entirely new structure developed by the oospore, and in no way homogenetic or even homologous with the gametophyte. It has been noted that the argument drawn from apogamy in favor of homologous origin finds little or no application among bryophytes, for the origin of the sporogonium seems to be as fixed as the origin of any plant structure can be.

It has been common to regard the distinct sporophyte as having been established once for all by the bryophytes, and the sporophytes of the higher groups to have been derived from those of the bryophytes. In searching for the origin of the leafy sporophyte, therefore, attention has been focused upon the sporogonia of bryophytes, and the Anthoceros forms have been selected as most nearly representing the ancestral condition.

The doctrine that any plant structure, however important, can have but one phylogeny, is hardly tenable at present. That heterospory has appeared independently in several lines has become evident ; and that it has resulted more than once in seed formation is hardly less evident. The conditions which determined these modifications must have been common enough to have established similar results more than once. Why the sporophyte may not fall in the same category is not clear. Professor Bower's statement that the polyphyletic origin of a structure is an easy escape from difficulties suggests caution, but does not close the door to the fact that nature may have found the same easy way out of difficulties.

In contrasting the sporophytes of bryophytes and pteridophytes, they seem to have nothing in common except that they are usually derived from the oospore and represent an asexual generation. These facts are important, but so are the numerous other facts in which they differ sharply. There are also asexual

generations derived from oospores among thallophytes, but regular alternation of sexual and asexual generations is not definitely established. When alternation becomes definite the sporophyte is a recognizable structure, but that this structure must have been established just once or in just one way is far from necessary.

It may be well to contrast the leafless and leafy sporophytes. In the former case the structure is never independent of the gametophyte, develops no lateral members, has nothing comparable to sporangia, and its whole tendency is to render complex the spore-producing region. In the latter case the sporophyte is dependent upon the gametophyte only in its embryonic stage, develops prominent lateral members, has distinct simple sporangia, and its whole tendency is to render complex the sterile or nutritive tissues. As one traces the evolution of the bryophyte sporogonia they give evidence of increasing complexity and hence rigidity, and little promise of originating such a diverse tendency as that shown by the sporophyte of pteridophytes. The mosses are conceded to be a highly specialized, and hence non-productive line, the legitimate outcome of the whole bryophyte tendency. Why the liverwort lines may not also be regarded as highly specialized and hence non-productive does not seem clear. It is true that the Anthoceros forms show a sporophyte tendency unlike the others, and that if such a sporophyte should become independent and put out leaves, and if the continuously developing spore region should be restricted and broken up into simple sporangia which should associate themselves with the leaves, we might have something like the existing leafy sporophytes. But there is no evidence that these things ever happened. On the contrary, the sporophyte of Anthoceros would seem to be as hopelessly specialized as that of other lines. It is true that all the things referred to above may have happened, and Anthoceros may be the nearest living suggestion of the archetypal pteridophyte, but the case is not so clear that our eyes should be shut to other possibilities.

If the bryophyte sporogonium is responsible for the leafy

sporophyte, then it is evident, as Bower has shown, that the leaves of the latter are the result of progressive sterilization, and are secondary structures of the sporophyte. But if some other origin of the leafy sporophyte is possible, the leaves may not have arisen as secondary structures.

It may be well to trace briefly the origin of gametophyte leaves, as exhibited by the mosses, since the sequence of events seems fairly clear, and may prove suggestive. Among the Riccia forms the thallose body produces sex organs and does chlorophyll work with no special differentiation of regions. From this condition there is evident a tendency to segregate the sex organs into definite regions, so that eventually the region of the body devoted to sex organs becomes quite distinct. The differentiation of a sex organ region is still further emphasized by its separation from the rest of the body by being carried up upon a vertical branch, an extreme case being displayed by Marchantia. As a result, the chief chlorophyll work and the production of sex organs are distinctly set apart by the organization of a gametophore arising from the thallus.

The gametophore, primarily a sex organ branch, proves to be more favorable for the display of chlorophyll tissue than the thallus, and the simple leaves of mosses appear, supplementing the chlorophyll work of the thallus. In sphagnums the thallose body continues associated with the leafy gametophore. In the true mosses, however, the chlorophyll work of the gametophyte is more or less given over to the gametophore leaves, and the thallus region is reduced to the so-called "protonema." In a very true sense, therefore, the gametophyte is always a thallus, special vertical or radial branches being developed in liverworts as gametophores, and in mosses as leafy gametophores. The loose habit of homologizing the leafy "moss plant" with a liverwort thallus on the one hand, and a fern prothallium on the other, is not merely bad morphology, but is apt to be very misleading.

The suggestion to be obtained from this history is that leaves may develop in response to more favorable conditions for their work, and such development may result in the great reduction

of chlorophyll work done by the less favored region, and its consequent simplification. It is evident that with the exchange of an aquatic for a terrestrial habit the thallose body would not be a favorable type for chlorophyll work, and that the development of chlorophyll tissue upon erect structures of various kinds might follow. Among bryophytes the erect structure laid hold of is the gametophore, and not the sporogonium. I grant that this same reasoning would make the sporogonium of the Anthoceros forms a specially well adapted erect structure for the development of leaf tissue and hence leaves. The objection, however, is that the sporogonia of bryophytes are most persistently spore-bearing structures and nothing else, every tendency towards more complex organization having spore production and spore dispersal in view; and that such specialized structures are not apt to be productive of new lines of development.

In considering, therefore, whether it is possible to disregard the bryophytes in our search for the origin of the leafy sporophyte, we are largely influenced by the fact that the bryophyte sporophyte, throughout its whole history, is dominated by a tendency which does not appear in the pteridophyte sporophyte. Before the establishment of alternate generations the plant body may be said to have had three functions, namely, chlorophyll work, and the production of gametes and spores. The appearance of the bryophyte sporogonium was dominated by the separation of spore formation from the other functions, chlorophyll work being retained by the gametophyte, along with gamete production. Attention has been focused so long upon the gametes and spores as the two dominant factors in differentiation that it is hard to conceive of the possibility of the domination of another factor. It is entirely conceivable, however, that another form of differentiation may have occurred, dominated by the needs of the chlorophyll work, and not by spore production. Certainly a great need for change, when aquatic conditions were exchanged for terrestrial, was in connection with the display of chlorophyll tissue. It would seem as if the bryophytes had laid emphasis upon spore production, and therefore never became

organized for the fullest use of terrestrial conditions; while the pteridophytes laid emphasis upon chlorophyll work, and became highly organized for terrestrial life. It would seem possible, therefore, with the three factors to take into account, that two distinct asexual lines may have been organized, distinct in the factor selected to dominate.

Such a conception may be simple enough, but it is hardly worthy of consideration without more practical statement. If more favorable structures can be developed in response to the needs of spores or gametes, there seems to be no good reason why more favorable structures may not be developed in response to the needs of chlorophyll work. If such a response in structure is possible, it would naturally express itself first in developing the largest display of chlorophyll tissue in the most favorable region of the body, which would gradually become differentiated more and more distinctly from the rest of the body. It does not seem clear why the appearance of an erect leafy axis, bearing neither gametes nor spores, is not quite as supposable as the appearance of a sporophore with neither gametes nor leaves, or a gametophore with neither spores nor leaves.

Of course such a leafy axis would be an integral part of the thallus body from which it was developed, and in no sense a distinct "generation," any more than the leafy gametophore and the protonema of mosses are distinct generations. Upon such a leafy axis spores would find a more favorable position than upon the ordinary thallus body, and eventually they would be segregated upon the leafy axis, developing in connection with chlorophyll tissue just as they had in the thallus body. In such conditions comparatively simple sporangia would be developed, being entirely subordinated to the nutritive tissues. A parallel case is found in the gametophore of mosses, which also prove favorable for leaf development; or even in the sporogonia of certain bryophytes, which also prove favorable for chlorophyll tissue, but this is rigidly subordinated to the work of spore production.

With the development of a leafy axis bearing spores, there is

no reason why it should not become independent of the thallus body which produced it, as the leafy gametophore of mosses becomes independent of the protonema. The great difference in the final result in the two cases arises from the fact that in mosses the protonema is without gametes or spores; while in the case we are supposing the thallus body produces gametes, and the leafy axis spores. That a thallus body can directly produce just such a leafy axis bearing spores is testified to by the numerous cases of apogamy observed among pteridophytes. In fact, the theoretical life history we have been tracing is concretely represented by the life history of a fern in which apogamy has occurred.

If the phenomenon of apogamy represents the primitive status of the leafy sporoyhyte, it remains to imagine how this spore-bearing leafy axis could have become the usual product of the oospore. We find no trouble in believing that the usual oospore product frequently appears apogamously, for this has been demonstrated; but to imagine a general primitive apogamous habit of origin gradually passing into a predominant oospore habit of origin is difficult. In the condition supposed, namely, a thallus body producing gametes, and a special leafy axis bearing spores, zygotes and spores would have the same power, the germination of each resulting first in the thallus body and afterwards the leafy axis. If real alternation can be brought about by such a condition, the thallus portion of the zygote product and the leafy axis portion of the spore product must be gradually eliminated. In other words, the tendency would be to eliminate that particular region which is concerned in producing the reproductive body. Perhaps such a tendency is no more difficult to understand than the fact that a spore produces a gametophyte rather than a sporophyte, and a zygote produces a sporophyte rather than a gametophyte. A common explanation has been that a zygote, for some reason, stops reproducing the plant body which organizes it, and begins to produce an entirely new structure, which certainly seems to have been the case in the formation of the sporogonia of bryophytes. It would seem no

more difficult for a zygote to stop producing one distinct portion of the plant body, and to continue producing the other.

Why in both cases it tends to produce the structure less immediately related to it, rather than the one which has originated it, is a question which cannot be answered at present. Cytology may offer certain suggestions, but they are vague as yet. The fact that the chromosomes are doubled in number by the process of fertilization, and are reduced again in the sporogenous tissue may have some bearing on the question. It seems clear that in all life histories where the sexual act occurs there must be a corresponding reduction division somewhere. In distinct alternation of generations, the "doubling" and the "reduction" are associated with the two generations. But before distinct alternation was established "doubling" and "reduction" must have occurred, and there is no present reason to doubt that in such case reduction often, if not generally, occurred in connection with the development of spores. When, therefore, the zygote was restricted to one region of the body, and the spore to a very distinct region, the alternation of "doubling" and "reduction" might well develop into an alternation of generations.

The very interesting results obtained by Strasburger and Farmer in their study of Fucus, which show that the reduction division in that plant occurs in connection with the development of the sex organs, may be correlated with the absence of spores. Such an observation emphasizes the fact that reduction must occur somewhere, and if sporogenous tissue is not developed, it would seem more likely to occur in gametogenous tissue, representing a new cell sequence, than in ordinary nutritive tissue.

With such an origin of the leafy sporophyte, it would follow that foliage leaves are not secondary, but primary structures, and that sporophylls have arisen from the differentiation of foliage leaves bearing sporangia, a state of things certainly suggested by the most primitive pteridophytes known. It would further follow that the evolution of the strobilus has followed the development of foliage leaves, a view in accordance with the older morphology. Such a view would make intelligible the

great "gap" recognized as existing between bryophytes and pteridophytes, as the two groups would not be phylogenetically connected, and would have developed along very divergent lines from the first. It would mean that at least two independent sporophyte lines have appeared, the bryophyte line probably with an antithetic origin, and the pteridophyte line possibly with an homologous origin. The great prominence of the latter line, with its spermatophyte sequence, is correlated with the development of a vascular system, and it would seem as though the evolution of an elaborate vascular system must have depended upon the domination of chlorophyll work.

Perhaps one of the strongest arguments against the polyphyletic origin of archegoniate plants is the constant character of the archegonium. It would seem to some inconceivable that an organ so definite and so characteristic, and so unlike anything in thallophytes, could have appeared in two independent lines. However, the possibility of two independent appearances of such an organ would depend upon its origin, a subject of great obscurity. That it has been derived in some way from the oogonium of thallophytes seems hardly to be questioned, and that it is one of the results of the exchange of aquatic for terrestrial habits seems hardly less doubtful. That the archegonium represents a group of oogonia protected by a layer of sterile tissue seems to be a reasonable suggestion, and that the differentiation of this sterile protective layer into neck and venter would follow naturally from the exclusive functioning of the innermost oogonium seem probable enough. The conditions which induced this protection of aggregated oogonia, however, could hardly be claimed to have resulted but once in an archegonium.

It must be acknowledged that if the leafy sporophyte has had any such origin as has been indicated above there is no algal evidence that can be presented, as in the case of the leafless sporophyte. It must be remembered, however, although it may be regarded as a convenient refuge for all theories of phylogeny, that we are dealing with a structure whose origin is very ancient. Why the algæ continue to give suggestions as to

the origin of the bryophyte sporogonium, and, so far as known, give no intimation of the independent origin of the leafy sporophyte, is a pertinent question. It seems to be also true, however, that the bryophytes give no clear suggestions as to the origin of the leafy sporophyte, and we are left to imagine the method of its origin from either group.

In thinking of this possible disconnection of the bryophyte and pteridophyte lines, it may be well to recall the similar experience of the gymnosperm and angiosperm lines. Certainly the gymnosperms and angiosperms seem to have more characters in common than do the bryophytes and pteridophytes, and seem to be more insistent in their demand for a common phylogeny; yet that the gymnosperms represent at least one independent phylum can hardly be longer doubted.

All such discussion is, of course, very vague and general, and may not commend itself to many as profitable. But it serves its purpose in stating the problem, and in presenting the possible alternative solutions. We have been in danger of restricting the operations of evolution too rigidly, making the lines of advance too few, and forgetting the possibilities of change during the enormous stretches of time. The polyphyletic origin of similar structures and of similar groups makes the problems of phylogeny immensely more complex, but is probably much more consistent with the facts.

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